GROWTH STUDIES IN FOREST TREES

I. PINUS RIGIDA MILL[1]

HARRY P. BROWN

(WITH PLATES XXIV AND XXV)

The phenomenon of tree growth has long been a subject of investigation. SACHS, HUGO DE VRIES, NÖRDLINGER, MER, the HARTIGS, WIELER, BÜSGEN, VON MOHL, and a host of others have worked on problems concerned with it, and many papers presenting the results of investigations are to be found in the literature of the last half-century.

As might be expected, the question has resolved itself into a number of minor topics, each with its coterie of followers. Some have placed particular stress on spring and summer wood formation; others have studied growth as related to external factors or to inheritance. Various instruments have been devised to measure tree growth, and one author (REUSS **12**) goes so far as to assert that thunderstorms cause a growth stimulus in trees. Investigations dealing with every phase of the subject are described in exhaustive detail, and yet with rare exception there is a maze of conflicting opinion sufficient to confuse even the careful reader.

The present studies were undertaken with a twofold purpose, namely, to clear up disputed points regarding annual ring formation in trees and to formulate laws of tree growth. Investigations were carried on upon various forest trees with this idea in view. The results of those on *Pinus rigida* are embodied in this paper.

Secondary thickening in trees arises as a general rule from a cambium which lives from year to year. This annually passes through certain active and certain dormant periods. The latter assertion, however, is to be taken in its broadest sense. In many tropical woods the interruption to growth can be detected only with a microscope, while in others it is totally lacking; the wood appears

[1] Contribution from the Department of Botany, Cornell University. No. 148.

as a homogeneous mass. The formation of this cambial layer takes place the first year, and is brought about by the linking together, so to speak, of the fascicular cambium of the primary bundles by the formation of interfascicular cambial zones, the result being a cylinder of merismatic tissue capable of division. There are, in addition to this, however, certain other growth phenomena. In the cortex of many trees, either near or remotely distant from the primary cambium, secondary cambial zones arise, whose function it is to form cork, the so-called cork cambiums. They are not united in a ring, as is the primary cambium, but extend for comparatively short distances in a peripheral direction.[2] Again, as met with in the Cycadales and Gnetales (COULTER and CHAMBERLAIN 4), successive bundle-forming cambiums sometimes arise toward the periphery of the stem, and in such cases the life of the primary cambium is generally very short. Further, among dicotyledons there are a number of modifications of secondary thickening, particularly in underground parts. In the present studies, however, it is the intention to confine investigation to growth as it normally occurs in trees, that is, to the activities of a cambium which has certain active and certain dormant periods.

A number of specimens of *Pinus rigida* in the Cornell pinery as well as others in the wild state were used. Those in the nursery consisted of a number of individuals standing in a row which ran approximately east and west. The land sloped gently to the southwest and drainage conditions appeared to be good. The individual trees were about 22 years of age and seemed to be in a thriving condition. The height varied from 6 to 7 m., depending on the vigor of the individual, and the average diameter at breast height was 12 cm. In 1909, when investigation began, the branches extended to within 1.2 m. of the ground. However, during the year above mentioned, the trees were pruned to a height of 1.9 m. above the ground. Experiments were carried on with six individuals of this series, which were numbered I–VI.

The trees in the wild state had better be described separately, since each was of different age and external factors varied with the individual. For the sake of clearness they were designated as

[2] Exceptions to this rule occur, resulting in the so-called "ring-barked" trees.

A, *B*, and *C*. These specimens were growing in a strip of woodland about one mile north of the university campus. Conditions of soil and light appeared to be good in every case, that is, to all appearances the trees were not retarded.

Tree *A* was a magnificent specimen about 25 m. high; in other words, it had practically reached its maximum size. The trunk was slightly shaded to a height of 4.5 m. by an undergrowth composed of white pine. There were no branches above for 18 m. until the crown began. The latter was but fairly developed, being about what one might expect under forest conditions. At breast height, the caliper measure was 50 cm. A conservative estimate of the age would be 100 years.

Tree *B* was a younger individual. Its height was approximately 20 m., and crown development had progressed but poorly. At breast height the caliper measure was 26 cm. The base was entirely free of undergrowth, and light conditions were better inasmuch as there were no close neighbors. Tree *B* then differed from tree *A* in (*a*) age, (*b*) light conditions, (*c*) crown development, (*d*) height, and (*e*) diameter.

Tree *C* was about the age of those in the nursery, namely 20–25 years, and rose to a height of 7 m. Branches were borne practically to the ground. The caliper measure was 11 cm. Illumination was better on the south side, due to the close proximity of a road, while on the north the underbrush encroached slightly.

Methods

Investigations began in the spring of 1909, and the last cutting that year was made on July 6. Alternate cuttings were taken from two different individuals at intervals about a week apart, so that two weeks elapsed between incisions on any one tree. These were made in the following manner. Beginning from the base of the apical shoot, portions of the cortex and wood to a depth of at least one annual ring were removed at intervals of about 50 cm. Twelve cuttings were made in this manner with the aid of a sharp pocketknife, care being taken not to rupture the cambium. Each cutting was placed in a separate vial, properly labeled with the date, num-

ber of cutting, and tree, and kept separate from the others in all the successive processes of fixing and imbedding.

The following year (1910) cuttings were again resumed on the same trees, as well as on four more in the same row. The manner of procedure was identical with that above described except (*a*) every other cutting was omitted and (*b*) this season the first cutting was made February 21, the second April 2, and thereafter until the third of May. The object was to check up the results of the previous season and to make new observations. Two cuttings were also made on trees *A*, *B*, and *C* on April 27, one on the north side and one on the south. For purposes of comparison, one root cutting was taken from tree III on the same date.

Microscopical characters of the wood

As is characteristic of the Coniferae, the secondary wood of *Pinus rigida* is entirely devoid of vessels. It consists almost entirely of tracheids with bordered pits on their radial walls. In cross-section these appear regularly arranged in radial rows, which occasionally divide as they proceed toward the cambium. In longitudinal section they present the normal tracheid form, that is, a rectangular prism with sloping ends. The annual rings are sharply differentiated. Proceeding from the pith outward in radial direction are numerous pith rays; secondary rays arise in response to necessity; both are of the usual coniferous type. The histological characters of coniferous wood, however, have been described in detail by PENHALLOW (**11**), and the reader is referred to his excellent work for further detail.

The structure of the secondary thickening in the roots is quite closely related to that of the stem. However, there are one or two differences. The demarcation between the different rings is not so sharp. This results because the wood of the root is less dense than that of the stem. The tracheids possess wider lumina and there is less summer wood produced. In radial section the bordered pits on the walls are often biseriate, a condition which is never met with in the wood of the aerial portion.

Microscopical characters of cambium and cortex in winter condition

CROSS-SECTION

The radial rows of tracheids in the xylem continue directly out into the cortex (fig. 9) through the cambial zone. For a time this radial arrangement is maintained, but sooner or later it becomes irregular, due to certain changes which take place. The cambial zone in cross-section appears as a number of layers of cells with comparatively thin walls. It is impossible to pick out the initial layer. Exterior to this are the sieve tubes. These have wider lumina than the cells of the cambial zone, and the walls are thickened as much as or more than those in the summer wood section of the xylem. However, they are not lignified as are the latter. Companion cells are wholly lacking. The rows of bast parenchyma are very prominent. One row with a few scattered individuals is formed each year (STRASBURGER 13), so that the thickened layers of sieve tubes are separated by thin bands of bast parenchyma. In the outer cortex the bast parenchyma cells become gorged with starch and greatly enlarged. As a result the older sieve areas are stretched tangentially and are seen as thin bands separating the larger cells. Pith rays appear as straight lines running out into the cortex, but as they proceed radially into the cortex they soon become more or less irregular and curved. There are no crystallogenous cells such as are described by STRASBURGER in *Pinus silvestris*. Exterior to the cortex proper there is a series of corky layers which have arisen from living cells in the outer cortex, the so-called cork cambiums. Their structure is of the general type described by STRASBURGER (13).

RADIAL SECTION

In radial section the cambial cells appear as prisms with sloping ends. The size varies slightly with the age. The sieve tubes have the general shape of the cambium cells from which they originate. Their radial walls are equipped with sieve plates, and these have the same location as the bordered pits on the walls of the tracheids. In radial section likewise we see to best advantage the bast parenchyma. This consists of rows of barrel-shaped cells arranged one

above the other. There is also a change in the pith rays. The ray tracheids have given rise to ray cells, so that the pith rays consist exclusively of the latter. These as well as the bast parenchyma cells contain abundant starch.

TANGENTIAL SECTION

In order to study cambium and cortex in tangential section, a series of mounts is necessary. The same general characters are observable, but in addition it is evident that there is an entire absence of sieve plates on the tangential walls of the sieve tubes. The callus thickenings of those on the radial walls, however, are particularly noticeable with proper staining (methyl blue).

Cambial awakening

In taking up the study of xylem formation as it normally occurs in trees, one naturally begins the study before cambial activity begins. Cuttings taken at different heights from tree III on February 21, 1910, all showed in cross-section the general outline of the completed ring. Growth was not manifest in any of the sections. Each ring presented well marked areas of early and late wood. The latter in *Pinus rigida* is sharply differentiated, owing to its greatly thickened walls. The above statement does not hold true, however, for the wood of the first two or three years at any point in the trunk. Here there is no sharp demarcation between early and late wood. This condition is probably brought about by the fact that the main axis was elongating rapidly at this point when the ring was formed, or else, as these investigations tend to show, growth is slow in beginning in the apical shoot but progresses very fast when once started, so rapidly in fact that there is not sufficient time for the walls to thicken appreciably. In either alternative, there is a gradual thickening in the walls of the late wood of successive rings as the apical shoot progresses aloft.

The next set of cuttings were taken on April 4, 1910, from tree III. The cambium was still in the resting condition. Figs. 1–3 and 7–9 show the changes which occurred (figs. 1–3) between April 4 and April 15. In fig. 3 growth is more advanced than in either figs. 1 or 2. The latter are both in the resting condition. So far

as can be detected there is no evidence of tracheal formation. Figs. 7–9 are from cuttings made on the same individual at this time, but each successively nearer the ground. In the first two growth is in evidence, while in the last the cambium is still in the resting condition. It is evident from the photographs that in the spring of 1910 growth made itself manifest in tree III as early as April 15. Cuttings taken from trees IV and V at the same date likewise showed evidence of cambial activity. While there was no satisfactory evidence obtained the previous year as regards cambial awakening, since observations were begun too late, sections from tree II on May 13, 1910, showed growth in such an advanced state that cambial activity must have begun fully as early the previous year.

As regards cambial awakening in trees *A*, *B*, and *C*, no lengthy observations were carried on; but two cuttings per tree were made on April 27, one on the north side and one on the south. At this date trees *B* and *C* already showed evidences of growth at breast height in both cuttings. In tree *A* the cambium was still in the resting condition. However, tree *A* was older and taller than the other individuals, and it is very evident that growth must have already begun in the higher parts.

The observations described above are in accord with those of other investigators. Büsgen (**3**) gives the time in general for cambial awakening for middle Germany as between the last half of April and the first half of May. R. Hartig (**7**) has observed that evidences of growth are manifest in young (10 years) specimens of *Pinus silvestris* as early as April 20, while its appearance at the base of the older trees depended very much on external factors, such as thickness of stand, soil conditions, ground cover, etc. Buckhout (**2**), by means of bark measure, gives the date of growth inception in larch and white pine as the last week in April. However, as his computations were made at the base of the trees, probably growth began aloft earlier. That growth was not evidenced at the base of tree *A* was due, according to the researches of R. Hartig (**7**), to at least three causes, namely (*a*) long trunk, (*b*) age, and (*c*) shaded base. While the present investigations do not afford conclusive evidence, inasmuch as they covered but a

period of two years, it would appear that in the vicinity of Ithaca growth began in *Pinus rigida* at about the same time each spring. To determine this point definitely, however, observations must needs be carried on for a period of years. That growth made itself evident in 1910, however, as early as April 15 is readily apparent from the photographs.

Place of cambial awakening

The question of origin of growth is still in dispute. T. HARTIG (**8**) claimed that it made itself manifest in the youngest branches first and extended slowly downward. NÖRDLINGER (*Forest Botany*, 1874) makes the same assertion. R. HARTIG (**7**) appears to accept his father's statement if we are to judge from the following quotation: "Am oberirdischen Stamme beginnt der Zuwachs zuerst in den jüngsten Trieben," etc. These three investigators, therefore, were unanimous in the opinion that the awakening of growth is earlier at the top of a tree than below.

MER (**10**) disputes this general assertion. According to his researches, the procedure of awakening was sensibly different in older trees. While in 25-year-old oaks, beeches, and firs, growth was first manifest in the youngest branches, in the older trees it was in evidence at the same time at the bases of the branches and even in the trunk where the roots began. From these points growth gradually extended to the intermediate regions.

Figs. 4–6 correspond respectively to those of the preceding numbers, except that a period of 19 days intervened. Comparing those of different date, we see that growth is more in evidence in every case where the cutting was taken at the later date. In figs. 1 and 2 we have apparently the resting condition, while figs. 4 and 5 exhibit signs of growth, the latter being more in evidence in fig. 5. Comparing figs. 3 and 6, it follows that there is a considerable advance in growth. In the former, at the outside, only two half-formed tracheids are to be seen, while in the latter three or four rows are present and these are of larger size. Comparing figs. 1–6 as a whole, it is evident that during a period of 19 days there was an awakening of cambial activity in the apical portion, first manifest in fig. 3 on April 15. Growth first appeared in the crown of tree III

some distance below the apical shoot, but in a period covering 19 days gradually spread upward and was in progress in the apical shoot on May 4, 1910.

Cuttings of May 4 corresponding to figs. 7–9 were not photographed. Examination revealed the fact, however, that growth was in progress throughout the basal portion of the trunk on that date, and had progressed to a greater extent than was evidenced on April 15.

From the above investigations it follows that growth was in progress throughout the main axis of the tree on May 4, while 19 days previous it was not in evidence in either the apical portion or the base. If R. HARTIG is right in his assertion that growth is first manifest in the branches, *Pinus rigida* is surely an exception to the rule. MER'S investigations on *young* trees are in accord with HARTIG'S, so here likewise growth in *Pinus rigida* appears to present an anomaly. That HARTIG is right in his assertion that cambial activity proceeds from the base of the crown downward, investigations on trees *A*, *B*, and *C* seem to give convincing evidence. Cambial activity was already in progress on both sides of the base in trees *B* and *C* on April 27, while both cuttings in tree *A* on that date appeared to be in the resting condition. This is explained in that the trunk of tree *B* was better illuminated below than that of tree *A*, while tree *C* was but 25 years old. But at this date growth must have been in evidence in the upper portions of tree *A*, and the only reasonable hypothesis is that it had not yet reached the base, owing to poor insolation, thick bark, and age of the tree.

Growth in lateral branches

With a view of adding something further of value to the manner of growth procedure in *Pinus rigida*, investigations were also carried on upon certain of the lateral branches. Cuttings were taken from each year's growth until the main axis was reached. Then incisions were made 20 cm. above and a like distance below the point where the branch joined the main axis. Growth in the branches followed the same rule as in the main axis. It commences some distance back of the apical shoot and spreads gradually in both directions. Time of awakening in the apical shoots of the

branches, at least in the case of trees standing in the open, appears to be identical with that in the apical shoot of the main axis. Cuttings taken May 4 showed about the same amount of growth in each case.

The time of the beginning of cambial activity at the base of the branches is of interest when compared with that of the main trunk. Fig. 11 shows a section from the base of a limb six years old. Fig. 10 is from a cutting taken from the main axis just above the branch, and fig. 12 a like distance below. Growth is most advanced in fig. 12, present in fig. 10, but lacking to all appearances in fig. 11. Cuttings taken from the limb in question showed growth in evidence to the extent of one or two tracheids (out to and including the apical shoot). It follows from the above that growth at the base of the branches is more retarded than at neighboring spots in the main axis. It proceeds more rapidly in the latter than it does in the former, so that it is often in evidence in the main axis before it makes its appearance at the base of the branches. This may be due to the more rapid rise of solutions in the trunk, although further investigation is necessary to decide that point.

Rate of procedure

Having determined the general procedure of growth in *Pinus rigida*, observations were next made on the rate of procedure. In order to make estimates of this, the series of cuttings of 1909 on tree II were employed. There were four sets of these of twelve each. In each set the amount of wood formed for the individual section was determined as nearly as possible with a micrometer scale, and the results tabulated on a basis of 100 (table I). The number of days intervening between each observation are given as well as the total gain and average gain per day; *x* implies cutting was a failure; + signifies width at least as much as given; ? indicates apparent loss due to local growth fluctuation.

The table is of value in leading us to certain general conclusions. On May 13, the width of the new-formed ring was greatest in cuttings 4–6. It gradually dwindled in size toward the apical shoot, while below there appeared to be a decline followed by an increase. The next investigation was made on May 25, twelve days later.

TABLE I

No.	Amount	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day	Amount	No. of days	Gain	Gain per day
	May 13, '09	May 29, '09				June 3, '09				June 15, '09			
1	3	5	12	2	0.17	5	9	0	0.00	35	12	30	2.50
2	3	5	12	2	0.17	20	9	15	1.63	25+	12	5	0.42
3	8	8	12	0	0.00	24	9	16	1.78	*x*	12	*x*	*x*
4	12	15	12	3	0.25	40	9	25	2.78	35	12	?	?
5	12	18	12	6	0.50	30	9	12	1.33	40	12	10	0.83
6	12	20	12	8	0.67	30	9	10	1.11	35	12	5	0.42
7	8	13	12	5	0.42	40	9	27	3	40	12	0	0.00
8	*x*	10	12	*x*	*x*	30	9	20	2.22	38	12	8	0.67
9	8	11	12	3	0.25	40	9	29	3.22	45	12	5	0.42
10	6	10	12	4	0.34	21	9	11	1.22	30	12	9	0.75
11	*x*	*x*	12	*x*	*x*	25	9	*x*	*x*	42	12	17	1.42
12	11	8	12	?	*x*	*x*	9	*x*	*x*	17	12	*x*	*x*

Looking at the average gain per day, we see that in cutting 6 the greatest increase occurred, while above and below the amount of gain varied irregularly with the different cuttings. However, the gain in the apical shoot was but slight. Comparing the results of May 25 with those of June 3, it is evident that, with the exception of the apical shoot, the average daily increase at the latter date was greater in every case than in the former. In other words, the tree grew faster in diameter, with the exception of the terminal shoot, during the last of May and the first of June than before that time. It follows from the table that the rate of increase varies considerably with the cutting and obeys no general law. The data of June 15, however, are most interesting. There was a decrease in the rate of growth between June 3 and June 15, with the exception of the apical shoot. Here, on the contrary, the gain in 12 days was 15 times as great as that of all the diameter growth previous to June 3. There was then a very marked increase in the formation of the annual ring at this point as compared with the gradual decrease in the remainder of the tree. Unfortunately, however, data are not available bearing on the rate of elongation of the apical shoot. It would appear, however, that its elongation must have been very rapid up to June 3, so much so in fact that the increase in the width of the annual ring could not result. From June 3 to June 15 the rate of elongation probably decreased appre-

ciably, while greater increase of wood formation resulted as a natural sequence.

Before summing up the results of the preceding paragraph, some observation on cessation of cambial activity should be given. It has long been recognized that while cambial activity makes itself manifest in many trees at about the same time, there is no relation evident in its cessation. Thus BUCKHOUT (**2**) found in *Larix decidua* that there was little if any growth after July, while *Pinus Strobus* continued to form wood until well into September. R. HARTIG (**6, 7**) also gives data bearing on this subject. In beech it lasts 2.5 months, in oak 4 months, in Scotch pine and Norway spruce 3 months. FRIEDRICH (see WIELER **14**), on the contrary, claims that in coniferous and hard woods in general there are two periods of growth, one lasting until about the end of May, sinking until the middle of June, and reaching a maximum again in July. Complete cessation resulted by the middle of August. The majority of workers, however, unite with HARTIG in saying that cessation of cambial activity varies greatly with the species concerned.

In the present studies, the latest cuttings in 1909 were made on July 6 upon tree III. At that time growth was still in progress throughout. Comparing these with cuttings taken from the same tree on February 21 of the next year, the following interesting results are obtained. Cutting 2 showed 0.5 of the ring complete, cutting 4, 0.6, cutting 8, 0.85. R. HARTIG (**6**) agrees with T. HARTIG (**8**) that cessation of growth begins first in the crown in trees in open stand and proceeds gradually downward. If such is the case, the data just given present an anomaly, or else growth was accelerated in the apical portions after June 15. However some of HARTIG'S data are in accordance with that already given. For example (BÜSGEN **3**), on June 21 the ring of an oak as compared to that of a previous year gave the following data:

At 1.3 m. height........0.45 complete
At 3.5 m. height........0.45 complete
At 5.7 m. height........0.45 complete
At 7.9 m. height........0.72 complete
At 12.3 m. height........0.57 complete
At 14.5 m. height........0.56 complete (3–4 year branch)

HARTIG then obtained results comparable to the present ones; that is, at about the middle of June he observed that growth was most advanced near the middle of the tree and decreased in both directions from that point. And yet he persists in his assertion that growth ceases in trees in open stand first in the youngest branches. Such being the case, the only possible solution of the data given above is that there must have been a marked acceleration of growth in the apical portions after June 21 and a corresponding decrease in the parts below. Whether the same applies in the pitch pine further investigation must decide. There was an increase in radial growth in the apical shoot and at the same time a decrease below between June 3 and 15, but that growth ceased first above cannot be deduced from the present observations.

As regards the theory advanced by FRIEDRICH concerning two periods of maximum growth in trees, little can be said. The second period if present in *Pinus rigida* must be the minor one, inasmuch as the ring was on an average more than half completed on June 15.

Width of the ring

Measurements were made from sections of tree III to determine the width of the ring at different heights. According to HARTIG, in trees in open stand the amount of wood formed increases from apex to base. This may arise from one of two alternatives; either the annual ring may decrease in size owing to the increasing diameter, or the reverse may be true. The latter, he says, is but rarely the case and sometimes occurs in trees which are exceptionally well nourished, that is, those possessing a large vigorous crown. From these observations it is to be expected that in *Pinus rigida* the ring would increase perceptibly in width toward the base, inasmuch as the crown is as a rule not exceptionally well developed. Such was the case. At cuttings 1 and 4, the completed ring on February 21, 1910, was about the same width. At cutting 8 it was but 0.85 the size of that above, while cutting 12 showed a still further decrease to 0.70. It follows that in *Pinus rigida*, if there is such a decrease in the size of the ring from apex downward in young vigorous growing trees, the same applies with even greater force in older trees with longer axis and poorly developed crown.

The living portion of the cortex, on the contrary, follows a law exactly the reverse. In the upper portions of the crown the cortex is necessarily thin, inasmuch as it contains a relatively small series of bast parenchyma and sieve tube areas. Below, the thickness of the cortex increases markedly, so much so in fact that it often attains 3–5 cm. in width. The storing capacity of the cortex as a result must be greatest in the basal portions of the trunk. Assuming that food abundance alone was concerned in cambial awakening, the latter would result first below. Inasmuch as it does not, there are certainly other determining factors, chief among which is probably insolation.

Investigations on the older trees revealed a number of factors of sufficient interest to demand mention in this paper. A curious feature long known to former workers was especially prevalent. I refer to the often noted lessened density of the wood on the south side of trees. This is due to the fact that the proportion of summer wood on the north side is greater as compared with the width of the ring than on the south side. This disparity in wood formation, however, is not so marked in young individuals. The ring formation is much more regular and it is only in the older trees that the phenomenon above described is seen. As to the cause of this lessened density on the south side, no reasonable conclusion was attained in these investigations, nor has it ever been satisfactorily accounted for. It is without doubt correlated with insolation in some way, but further study is necessary to determine this definitely.

The manner of cambial awakening likewise presents an interesting study. It was observed that even on different sides of the same section a noticeable disparity often occurred. In some cases growth had proceeded to the extent of one or two partly formed tracheids, while in closely neighboring spots the cambium appeared as yet in the resting condition. Nor was one tracheid completely formed as to size before another began. Often rows of three or four small tracheids were visible, none of which had yet attained half the size of those formed first the previous year. In such cases it would appear that cell division was so rapid in the cambial region during favorable seasons that new elements were laid down before

their predecessors had yet attained their maximum size and strength.

Double rings were often in evidence in the old trees. These might easily cause miscalculation as to age. The phenomenon of double ring formation has often been observed, especially in broad-leaved trees. Here it was ascribed sometimes to partial or complete defoliation, at others to favorable or unfavorable external factors. The first assumption would not hold in *Pinus rigida* in this case or in general, since defoliation rarely occurs. The cause must be ascribed to external growth conditions, but what these are would be difficult to determine. That they are most prevalent in old trees is well known, and this would lead one to infer that their formation is in some manner correlated with inhibition of growth, since the effects of this are most marked on older less vigorous individuals.

Secondary thickening in the roots

Little stress was put on the study of secondary root thickening in the present investigation. Only one cutting was taken, on April 27, 1910, for purposes of comparison, so that no reliable deductions can be made. At this time cambial activity was not manifest, although it must have been in process throughout the aerial portion with the possible exception of the apical shoot. T. HARTIG (**8**) claimed that cambial awakening in the roots is much later than in the aerial portions. He gave midsummer as the time of first inception and said it continued far into October. Whether the same applies to *Pinus rigida* further investigation only can decide. Suffice it to say, however, that the growth in thickness of roots must not be confused with growth in length. The latter is manifest often as early as March and continues throughout the season.

Summary

1. The histological characters of *Pinus rigida* present no wide variation from the normal coniferous type.

2. The secondary thickening in the root is similar to that in the stem, but differs (*a*) in less sharp demarcation between the annual rings, (*b*) in the biseriate character of tracheids, and (*c*) in less density.

3. Growth began in young 20–30-year old specimens of *Pinus rigida* in the vicinity of Ithaca as early as April 15. While there was no direct evidence of cambial awakening secured the previous year, sections taken at a later date showed growth in such an advanced state that it must have begun fully as early.

4. In older trees cambial awakening is sometimes retarded at the base where proper insolation is lacking.

5. There is no appreciable difference in the time of cambial awakening on the north and south sides of trees.

6. Growth began first in 20–25-year-old specimens at some distance below the apical shoot, but during a period of 19 days gradually spread upward until it reached the apex of the trees.

7. Investigations on trees *A*, *B*, and *C* tend to show that growth in older individuals begins first in the crown and spreads downward. The time of its inception at the base varies with conditions of insolation, bark, etc.

8. Growth in the branches follows the same rule as in the main axis. The time of awakening in the former is almost if not absolutely identical with that in the latter.

9. Growth spreads down the main axis faster than it does along the lateral shoots.

10. Except in the terminal shoot, growth in diameter was more rapid between May 25 and June 6. In the terminal shoot itself greatest rapidity of growth was manifested between June 6 and June 15.

11. No reliable deductions concerning cessation of cambial activity can be drawn from the present investigations.

12. The width of the complete ring decreases from apex to base; the living portion of the cortex follows the reverse rule.

13. A number of peculiarities already noted by others are prevalent in mature specimens. These are (*a*) lessened density of wood on the south side of trees, (*b*) irregularity of cambial awakening in closely neighboring parts of the same section, (*c*) successive formation of new elements before previous ones have reached their maximum size, and (*d*) double rings.

CORNELL UNIVERSITY
ITHACA, N.Y.

LITERATURE CITED

1. BRITTON, N. L., North American trees. 1908. p. 31.
2. BUCKHOUT, W. H., Formation of annual rings of wood. Forest Quarterly **5**:259. 1907.
3. BÜSGEN, M., Bau und Leben unserer Waldbäume. 1897. p. 62.
4. COULTER, J. M., and CHAMBERLAIN, C. J., Seed plants. 1901.
5. GOFF, E. S., The resumption of root growth in spring. Wis. Sta. Rept. 1898:220–228. *fig. 6.* 1898.
6. HARTIG, R., Das Holz der deutschen Nadelwaldbäume. 1885. p. 35.
7. ———, Anatomie und Physiologie der Pflanzen. 1891. p. 262.
8. HARTIG, T., Bot. Zeit. **18**:829. 1858.
9. HASTINGS, G. T., When increase in thickness begins in trees. Science, N.S. **12**:585. 1900.
10. MER, E., Sur les causes de variation de la densité des bois. Bull. Soc. Bot. France **39**:95. 1892.
11. PENHALLOW, D. P., Anatomy of the North American Coniferales with certain exotic species from Japan and Australia. Amer. Nat. **38**:243. 1904.
12. REUSS, H., Beitr. zur Wachstumsthätigkeit des Baumes nach praktischen Beobachtungsdaten des laufenden Starkenzuwachsganges an der Sommerrinde. Forstlich. Zeitschr. **2**:145. 1893.
13. STRASBURGER, E., Die Angiospermen und die Gymnospermen. 1879.
14. WIELER, A., Über die Periodizität im Dickenwachstum des Holzkörpers der Bäume. Bot. Zeit. **56**:262. 1898.

EXPLANATION OF PLATES XXIV AND XXV

FIG. 1.—Cutting taken from apical shoot of tree III April 15, 1910; cambium in the resting condition; ×50.

FIG. 2.—Same, but cutting taken about 1 m. from the apex; cambium in the resting condition; ×50.

FIG. 3.—Same, but cutting taken about 2 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

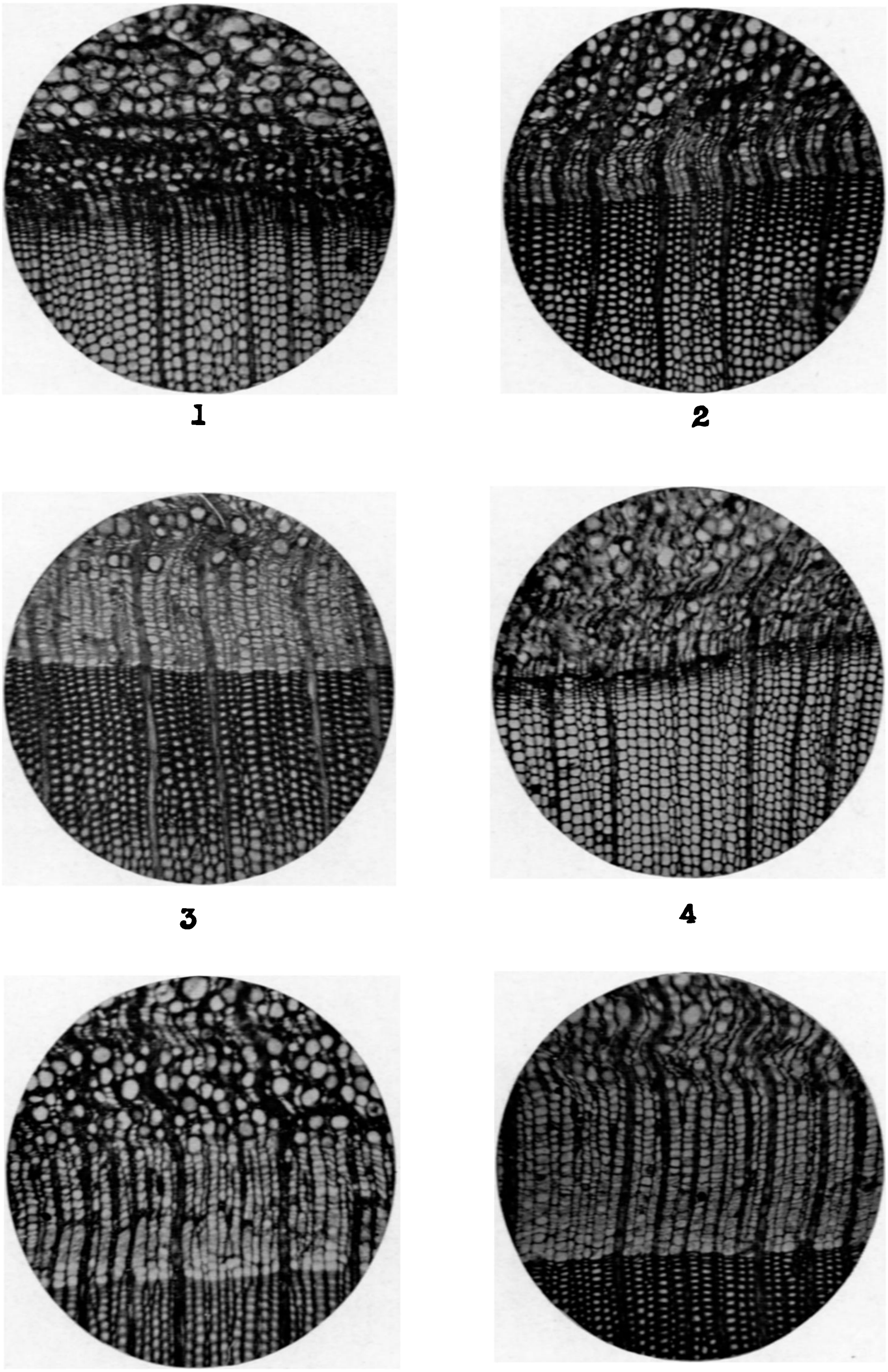
FIG. 4.—Cutting taken from apical shoot of tree III May 4, 1910; growth just beginning at *A;* compare with fig. 1; ×50.

FIG. 5.—Same, but cutting taken 1 m. from the apex; growth slightly more advanced; compare with fig. 2; ×50.

FIG. 6.—Same, but cutting taken from the apex; growth in evidence to the amount of 3 or 4 tracheids; compare with fig. 3; ×50.

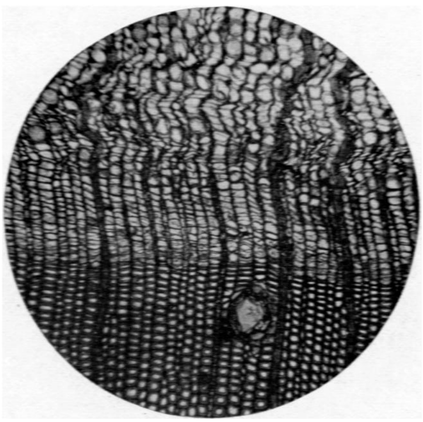
FIG. 7.—Cutting taken from tree III April 15, 1910, about 3 m. from the apex; growth in evidence to the extent of one or two partly formed tracheids; ×50.

FIG. 8.—Same, but cutting taken about 4 m. from the apex; growth in evidence to about the same extent as in fig. 7; ×50.

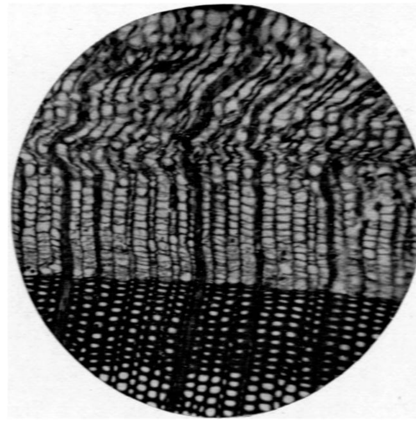


1 2 3 4 5 6

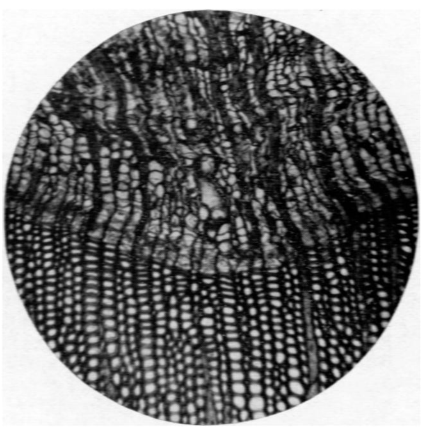
BROWN on PINUS RIGIDA



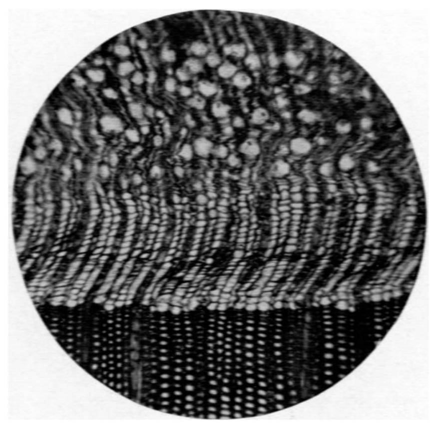
7



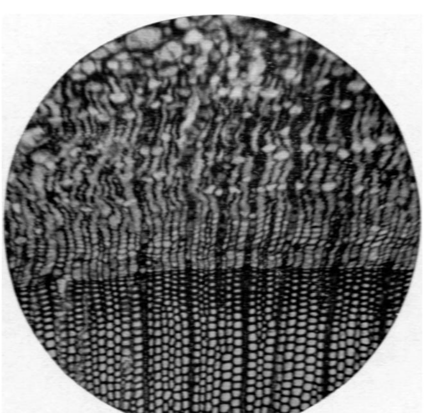
8



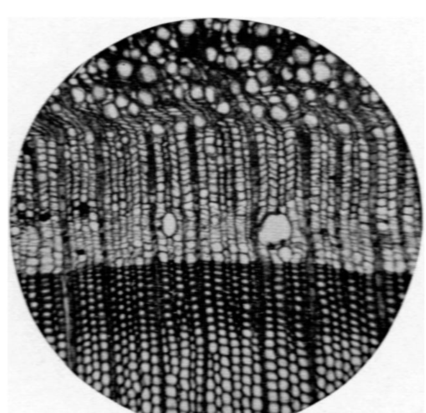
9



10



11



12

BROWN on PINUS RIGIDA

FIG. 9.—Same, but cutting taken about 5 m. from the apex; cambium in the resting condition; $\times 50$.

FIG. 10.—Cutting from main axis of tree VI April 22, 1910, at a distance of 3 m. from the apex; growth in evidence to the extent of several rows of partially formed tracheids; $\times 50$.

FIG. 11.—Same, but cutting from the base of a lateral branch which entered the main axis 20 cm. below cutting shown in fig. 10; no growth in evidence; $\times 50$.

FIG. 12.—Same, but cutting taken 40 cm. below that in fig. 10; growth in evidence to the extent of several rows of tracheids; $\times 50$.